14 Biomass and nutrient cycling by decomposer basidiomycetes

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Half a century ago Waksman was questioning the relationship between soil fertility and microbial activity. Since then much has been discovered about the influence of mycorrhizal basidiomycetes on plant growth and nutrient uptake, but we still know little about the involvement in mineral cycling of those basidiomycetes which are primarily decomposers of dead organic matter. Their supreme importance in the breakdown of cellulose and lignin is amplified in other chapters. This review discusses from an ecological viewpoint their biomass and influence on the cycling of nutrient elements other than carbon, particularly in temperate woodlands.

Biomass of decomposer basidiomycetes in litter and soil

On etymological grounds the term 'biomass' should be restricted to living matter, but frequent misuse has led to confusion. In this chapter it signifies, therefore, the total standing crop of an organism unless specified as being only living or dead, and 'production' is the biomass produced over a certain period of time.

The decomposer basidiomycetes rarely figure in lists of fungi isolated from litter or soil, even when their fruit bodies are abundant, and we still cannot obtain an accurate measurement of their total biomass in an ecosystem. We can, however, attempt to apportion biomass, within some ecosystems, to the various groups of decomposer and consumer organisms, and can obtain, as will be shown, some idea of the relative magnitude of the basidiomycete biomass.

It is an accepted fact that decomposition by heterotrophs is important in the release of nutrients for green plants and that heterotrophic metabolism forms a significant part of the total metabolism of a terrestrial ecosystem. Reichle (1977) estimated that heterotrophic metabolism (g C m^{-2} yr^{-1}) ranged from 34 to 57% of the total metabolism in forest, prairie and tundra ecosystems. Micro-organisms in general have a relatively high rate of production and turnover but a small living biomass; nevertheless the major proportion of the living biomass of the heterotrophic community of a temperate forest floor is microbial. Reichle, for example, attributed only 7% of the living heterotrophic biomass in a temperate *Liriodendron* forest in Tennessee to the pulmonates, nematodes and arthropods but 85% to the microflora. In a few ecosystems, the apportionment of biomass has been extended to the constituent groups of the microflora. For example, in the International Biological Programme analysis of Meathop Wood, an English deciduous woodland with a thin accumulation of litter and a mull humus on limestone, 96% of the microbial biomass in the leaf litter layer and soil (excluding woody remains and roots) was found to belong to the actinomycetes and bacteria, and only 4% to the fungi (Gray, Hissett & Duxbury, 1973; Frankland, 1975*a*,*b*, and unpublished). In terms of living biomass, which is more relevant to activity than this total biomass, the fungi had a much higher status, constituting 66% of the microflora. Attempts to subdivide microbial biomass usually cease at this point.

However, the type and distribution of fungal mycelium in a soil profile can be clues to the abundance of basidiomycetes, even if their species are rarely distinguishable unless fruiting. The distribution of the fungal biomass in the soil of Meathop Wood, estimated from hyphal length and classified as belonging to basidiomycetes or microfungi according to the presence or absence of clamp connections, is shown in Table 1, although it is recognised that the basidiomycete component may have been underestimated because the frequency of clamp formation varies between species. A relatively large quantity of non-basidiomycete mycelium (kg ha^{-1}) occurred in the lowest soil horizons. However, this reflected the sheer bulk of the subsoil. Fungal mycelium of all types was most concentrated (g g^{-1} substrate) in the thin organic L and (Oh + Ah) surface horizons, and basidiomycete mycelium, excluding as far as possible that of mycorrhizal and pathogenic species on and in living roots, was almost confined to this area of the profile, dominating the mycoflora during the decomposition of the cell walls of plant debris. As many as 89% of the dead *Quercus* leaves, which formed the principal component of the L horizon, were found by direct observation to be colonised by basidiomycetes 18 months after leaf-fall. Basidiomycete mycelium was also abundant on other leaf types in this

Table 1. *Comparison of the distribution of the biomass of basidiomycetes (kg ha^{-1} dry wt) with that of other microbial decomposers in the floor of a temperate deciduous woodland with mull humus (Meathop Wood, Cumbria, UK)*

Substrate or horizon		Basidiomycetes		Other fungi		Bacteria and actinomycetes	
		Living	Total	Living	Total	Living	Total
Woody debris		30.5	216.9	7.3	34.7	2.6	601.6
L	depth 36 cm	3.1	8.7	0.5	4.1	37.3	8433.3
(Oh + Ah)		8.9	31.7	3.4	12.9		
A		<1.0	<1.0	26.4	97.5		
B		<1.0	<1.0	31.4	155.6		
Dead roots		228.0	1628.5	65.1	325.7	8.0	1851.1
Total		271.5	1886.8	134.1	630.5	47.9	10 886.0

woodland, and the abundance increased with age of the litter (Fig. 1).

It is more difficult to classify hyphae accurately in litter after it has been homogenised as in the classic technique for measuring hyphal length (Jones & Mollison, 1948), but by using this method and converting length to biomass (see Frankland, Lindley & Swift, 1978) it was estimated that at least 68 and 71% respectively of the total fungal biomass in the L and (Oh + Ah) horizons of Meathop Wood (excluding roots) was of the basidiomycete type, closely resembling that seen on intact leaves. On this basis, basidiomycetes represented approximately one-eighth of the total fungal biomass in the litter/soil profile. The living biomass was also measured, assuming that hyphae with cell contents were alive (Frankland, 1975*b*). By this criterion, 36 and 28% respectively of the basidiomycete mycelium in the two organic horizons was living, i.e. approximately one-sixth of the living fungal biomass in the litter and soil of this woodland belonged to this group of fungi. The microfungi appeared to be represented by many more species, but basidiomycete mycelia characteristically are less ephemeral and accumulate more biomass than those of the microfungi.

Basidiomycetes can form therefore a significant proportion of the microbial biomass of a woodland soil, but their ecological importance in biomass terms becomes much more obvious if account is taken of the large quantities of fungal mycelium in dead wood and dead roots. In Meathop Wood, these substrates were often packed with mycelium, and many dead tree branches and roots contained virtually a 'pure culture'

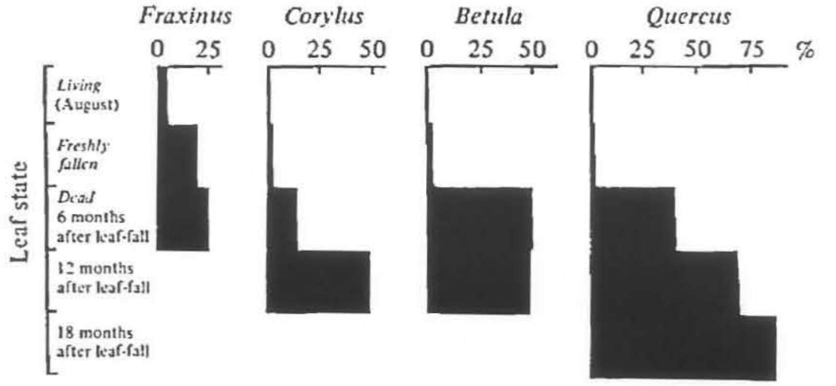

Fig. 1. Number of leaves (%) colonised by basidiomycetes (Meathop Wood, Cumbria, UK).

of a basidiomycete, such as *Stereum hirsutum* or *Armillaria mellea*. The total and living biomass of basidiomycetes and other fungi in the dead wood (M. J. Swift, personal communication) and roots are shown in Table 1. The mycelial content of roots was estimated from the weight of dead roots (J. E. Satchell, unpublished) by assuming that the fungal content was the same as in dead wood. According to these data on decomposer fungi, over 80% of all the mycelium and over 90% of basidiomycete mycelium on and in the forest floor was located in dead wood and dead roots, which suggests that research workers' past preoccupation with leaf litter in decomposition studies of woodlands may well have been misplaced.

The biomass of bacteria and actinomycetes is also included in Table 1, showing that they formed the major component of dead microbial material, but that basidiomycetes contributed at least 60% (272 kg ha^{-1}) of all living microbial biomass. However, all these estimates must be tentative until better methods of detecting these fungi are developed.

The annual production of the fruit bodies of the litter-inhabiting basidiomycetes of Meathop Wood was calculated from Hering's records (1966) to be only 1 kg ha^{-1} dry wt at most, so in this woodland the reproductive biomass of the basidiomycetes appears to be small in comparison with the estimates of their vegetative mycelium.

There is meagre information on the quantity of basidiomycete mycelium in other soil types, but the estimates for the calcareous mull in Meathop Wood are probably at the low end of the scale for temperate woodlands. Fungal mycelium in general is less concentrated in mull with a thin accumulation of litter than in mor with a well-developed litter

Table 2. *The proportion of clamp-bearing hyphae and dark pigmented hyphae in the profile of a Swedish forest podsol expressed as a percentage of the total length of fungal hyphae in each horizon: mean values, ($n = 6$).* (From Bååth & Söderström, 1977)

Horizon	Clamp-bearing hyphae	Dark pigmented hyphae
A_{00}	2	21
A_{01}	7	19
A_{02}	13*	14
A_2	7	15
B	5	27

* Significantly higher than in the other horizons, $P < 0.05$ (Bååth & Söderström, 1979).

layer. Witkamp (1960) confirmed this and found that, in autumn, 91% and 100% respectively of the mycelium in the upper 2 cm of the mineral soil of a calcareous mull and a mor under temperate oak forest was of the basidiomycete type. The total biomass of basidiomycete mycelium in a well-developed iron podsol under mature *Pinus sylvestris* in central Sweden (Bååth & Söderström, 1977, 1979) was higher than in the Meathop mull, although the length of hyphae with clamp connections as a percentage of the total hyphal length was somewhat lower. The highest proportion of basidiomycete hyphae ($P < 0.05$) was again near the surface in an organic A_{02} (H) horizon (Table 2).

Even less is known about the amount of basidiomycete mycelium in the soil of other climatic zones, but Flanagan & Scarborough (1974) reported that hyphae with clamp connections accounted for at least one-third of the total fungal biomass in some soils of the American tundra. Again, hyphae of mycorrhizal species may have been included with those of decomposer species; a lower proportion of basidiomycete mycelium was recorded in tundra soil lacking ectomycorrhizas by Miller & Laursen (1974). The biomass of saprophytic basidiomycetes might be expected to be greatest in tropical rain forests, which produce about three times as much organic matter as the most productive woodlands of the temperate region. This is unlikely, however, because the accumulation of litter is very small; on the other hand, higher temperatures and wet conditions result in speedy growth and decay, so mycelial production is probably much greater than in temperate woodlands.

Whereas biomass is the key to the capture of plant nutrients, the turn-over of this biomass is all-important in nutrient release, but as yet we cannot measure the annual production of basidiomycete mycelium in a natural soil. The only production estimate appears to be one obtained by the author for a single decomposer, *Mycena galopus*, growing on *Quercus* litter in Meathop Wood (Frankland, 1975*a*; see Frontispiece). It was determined by measuring changes in the biomass and decay rate of the mycelium on litter with a distinctive white rot, and was about twice the maximum biomass. The ratios of vegetative production:vegetative biomass:fruit body production for this species were approximately 10:5:1. If these ratios were extended to the other fruiting basidiomycetes of the litter, the mycelial production and biomass of the basidiomycetes in the L horizon became at least 10 kg ha^{-1} yr^{-1} and 5 kg ha^{-1} respectively. This biomass figure is of the same order of magnitude as the estimate obtained from hyphal length, but it is doubtful whether it is justified to extrapolate as far as this, considering the vagaries of fruiting and morphological differences known to occur among basidiomycetes.

Not only the vegetative mycelium but also the fruiting of basidiomycetes is more prolific in mor sites than in mull, as illustrated by Hering's survey of decomposer species in some English woodlands (Chapter 12). Coniferous woodlands are usually the most productive. Richardson (1970), for example, recorded 16–30 kg ha^{-1} yr^{-1} dry wt of agarics and boleti in a very thorough survey of a Scottish plantation of *Pinus*. These yields are still very low in comparison with commercial mushroom farming (Hedger & Basuki: Chapter 15), but Hora (1959, 1972) and others have obtained impressive increases of production by adding fertilisers to woodland soils. Again, comparative data from the tropics are lacking, but small decomposer species such as *Marasmius, Mycena* and *Leptonia* occur in large troops in the rain forests (Dickinson & Lucas, 1979; see also Singer & de Silva Araujo, 1979).

Basidiospores are so minute that their biomass is usually ignored, but their size is counterbalanced by the vast numbers produced (Buller, 1909; Kramer: Chapter 2). Hering (1966) recovered in one season 159 fruit bodies, many of them small species, from a 100 m^2 quadrat of the relatively unproductive Meathop Wood. This represents a total spore biomass of 0.1 kg ha^{-1} dry wt assuming that the mean number of spores produced by a fruit body was 1.0×10^9 (probably a conservative estimate!) and that the mean dry weight of a spore was 0.85×10^{-11} g (Cochrane, 1958). The contribution of basidiospores to the dispersal and release of nutrients is therefore likely to be of some significance in more productive woodlands.

Concentrations of mineral elements in decomposer basidiomycetes

Evidence that basidiomycetes can form a significant proportion of the microbial biomass of a woodland has been outlined. What does this biomass represent in terms of mineral nutrients?

Most information on the chemical composition of decomposer basidiomycetes in the field comes from analysis of sheets of mycelium stripped from wood or of rhizomorphs and fruit bodies. It is extremely difficult to collect sufficient quantities of unstranded mycelium from leaf litter and soil for this purpose. In addition, the chemical composition of fungi, including saprophytic basidiomycetes, is known to depend on their substrate (Levi & Cowling, 1968), so mycelium grown on synthetic media is not a reliable guide to the field state. Analysis of the mycelium of the litter decomposer *Mycena galopus* on an almost natural substrate was achieved, however, by laboriously stripping the hyphae from *Quercus* and *Corylus* leaf litter, which had been sterilised by γ-radiation and inoculated with the fungus without addition of nutrients (J. C. Frankland, unpublished). The concentrations of major plant nutrients (N, P, K, Ca, Mg) in this mycelium are compared in Table 3 with estimates for basidiomycetes growing in litter and wood obtained by other workers. Apart from some high levels of potassium and calcium, two elements which micro-organisms can absorb in luxury amounts, the concentrations of nutrients in the simple mycelium and rhizomorphs of the litter and wood decomposers were similar. In fact the concentrations of minerals in the *Mycena* mycelium on leaf litter were all within the ranges quoted for basidiomycetes on wood (Swift, 1977*a*).

In general, the fruit bodies of the litter decomposers (Table 3) were richer in nitrogen, phosphorus and potassium, and lower in calcium than their corresponding vegetative mycelium; potassium again occurred in luxury quantities. Stark's analyses (1972) showed similar trends in the nutrient concentrations of basidiomycetes from American sites, and her fruit bodies were consistently lower than rhizomorphs in calcium in both northern coniferous and southern rain forests. Fruit bodies of nonlignicolous species also tend, it seems, to contain greater concentrations of nitrogen, phosphorus and potassium than those of lignicolous fungi (Table 3; Vogt & Edmonds, 1980).

Spores as well as sporulating tissues are usually rich in the major

Table 3. *Comparison of the concentrations of mineral nutrients in undifferentiated mycelium, rhizomorphs and fruit bodies of decomposer basidiomycetes (% dry wt)*

	Litter decomposers						Wood decomposers	
Species . . .	*Mycena galopus*		Various[a]		Various[b]		Various	
Litter/wood type . . .	Broadleaved		Broadleaved		Broadleaved and coniferous		Hardwood and coniferous	
	Mycelium	Fruit bodies	Rhizomorphs	Fruit bodies	Rhizomorphs	Fruit bodies	Mycelium & rhizomorphs[c]	Fruit bodies[d]
Mineral nutrients								
N	3.50	5.70	4.13	4.40	—	—	0.23–4.31	0.72–1.13
P	0.24	0.69	0.93	1.00	0.16	0.55	0.02–1.31	0.19
K	0.57	4.47	3.16	4.90	0.39	2.52	0.16–0.61	0.39
Ca	0.95	0.17	0.85	0.11	3.93	0.04	0.68–9.50	0.96
Mg	0.37	0.12	0.14	0.13	0.04	0.05	0.04–0.88	0.21

Sources:
[a] Ausmus & Witkamp (1974).
[b] Cromack, Todd & Monk (1975).
[c] Swift (1977*a*): review data.
[d] N: Merrill & Cowling (1966); P, K, Ca, Mg: Cromack, Todd & Monk (1975).
—, not measured.

Table 4. *Ratios of the mineral nutrient concentrations, as percentage oven dry weight, of the mycelium of two decomposer basidiomycetes to the mineral nutrient concentrations of their substrates*

Mycelium . . . Substrate . . .	*Mycena galopus*[a] *Corylus* leaf litter	*Stereum hirsutum*[b] Living *Quercus* wood
Mineral nutrients		
P	2.9	9.4
N	1.8	8.2
Mg	1.2	4.8
K	2.0	3.0
Ca	0.5	1.9

[a] J. C. Frankland (unpublished data).
[b] Swift (1977*b*).

nutrients, but information on basidiospores is limited. Merrill & Cowling (1966) found that basidiospores of some wood decomposers contained 3% N, which was equivalent to the nitrogen concentration in the current hymenia of the same fruit bodies. Dowding (1976) pointed out that the nutrient content of fungal spores is unlikely to vary as much as that of mycelium, and that for any one species the content is likely to be largely genetically fixed.

As is typical of decomposers, many elements are more concentrated in saprophytic basidiomycetes than in the plant residues on which they are growing. This is illustrated by the concentrations of macronutrients in *Stereum hirsutum* on *Quercus* wood in relation to the concentrations in its substrate (Swift, 1977*b*), and except for calcium by those in *M. galopus* on *Corylus* litter (Table 4). The concentration factors were greater for the fungus on wood, which on a dry weight basis is relatively poor in nutrients, although, as Park (1976) emphasised, the nitrogen content as parts per million of wood with a moisture content of say 50% is not particularly low for decay organisms. Phosphorus was the element most in demand by both fungi. Vogt & Edmonds (1980) have also compared the nutrient concentrations in fruit bodies, including decomposer species, with those in litter. Although the nutrient content of fruit bodies in four distinct forest types of western Washington varied widely between species (e.g. 0.66–11.27% N), nitrogen, phosphorus and potassium were generally concentrated in significantly higher amounts in the fruit bodies than in the forest floor, but the fungi were not always linked in the analyses with their specific substrates. Evidence of wide variations

Table 5. *Comparison of concentration factors for mineral nutrients in decomposer basidiomycetes and decomposer insects on wood (ratios of nutrient concentration as percentage oven dry weight in the decomposer to that in the wood).* (After Swift, 1977*a*.)

Mineral nutrients	Ratio basidiomycete mycelium:wood	Ratio insects:wood
P	14.6	27.3
Ca	13.4	0.9
N	5.8	28.3
Mg	2.8	4.4
K	1.6	3.3

in concentration factors have been obtained from field experiments using radionuclides (Witkamp, 1969). The concentration of ^{137}Cs in fruit bodies varied from <0.1 to 80 times that in their tagged litter substrate, depending on the species of basidiomycete and season. There were also indications that the ^{137}Cs concentration increased with age of the long-lived fruit body of *Clavulina cristata* over a period of several weeks.

Among the micronutrients, significantly higher concentrations of molybdenum and zinc have been found in bracket fungi than in their supporting branches (Cromack, Todd & Monk, 1975). Similarly, higher concentrations of copper, iron and zinc have been recorded in fruit bodies and rhizomorphs than in their leaf and needle substrates (Cromack *et al.*, 1975; Stark, 1972). Sodium, essential to animals but not to plants and fungi, was also accumulated. Measurement of the concentrations of trace elements in the fruit bodies of a large number of higher fungi from natural habitats has also shown that these fungi often contain much more copper and zinc (parts per million dry matter) than living higher plants (Hinneri, 1975; Mutsch, Horak & Kinzel, 1979; Tyler, 1980). Hinneri's evidence also suggests that the fruit bodies of decomposer basidiomycetes are richer in minerals than those of mycorrhizal species.

Decomposer basidiomycetes have the potential therefore to be important accumulators of plant and animal nutrients, but they should be kept in perspective with other groups. Animals can have even higher demands for mineral nutrients as shown for wood decomposers (Swift, 1977*a*; Table 5), but their relative share in nutrient uptake will depend on their biomass and rate of turnover as well as on their nutrient concentrations.

'Capture' of mineral elements by decomposer basidiomycetes

Uptake of mineral elements from plant debris by a decomposer fungus will depend *inter alia* on the balance between available energy sources and mineral supply. Basidiomycetes are particularly well fitted to acquire both of these by virtue of their enzyme systems, ability to penetrate deeply, relatively large surface area, translocating powers, and longevity. Analyses of fruit bodies and their substrates in the field have provided evidence of their ability to tap distant sources of nutrients by translocation. Merrill & Cowling (1966), for example, found that nitrogen had not been stripped from wood adjacent to the fruit bodies of various polypores, and they calculated that the nitrogen required for sporulation must have come from very large volumes of wood or from sources outside the wood itself. However, without measurement, the actual uptake of nutrients in the field usually has to be assumed.

Once a nutrient element is incorporated within a micro-organism it is temporarily unavailable to plants and can be said to be captured or immobilised. The nutrient concentration and the biomass of the organism together provide an estimate of this nutrient pool. Witkamp (1969) calculated that gross immobilisation of the readily-leached mineral ^{137}Cs by the natural microflora on *Liriodendron tulipifera* litter could be as much as 60%. It is rarely possible, however, to estimate the size of the nutrient pool in a basidiomycete in field material with current methods, but Swift (1977*b*) has achieved it for *Stereum hirsutum* on decaying branch-wood. *Quercus* branches occupied solely by this species were chosen so that the fungal biomass could be estimated by hexosamine assay. Nutrient concentrations were determined by chemical analysis of the wood and of mycelium stripped from inside the branches. As decay advanced, the fungus gradually captured the nutrients until 90–100% of the nitrogen and phosphorus, and 30–50% of the calcium, magnesium and potassium were contained in the mycelium (Fig. 2). Lower proportions of nutrients were immobilised by *Mycena galopus* growing on sterilised *Betula* and *Fraxinus* leaf litter (Table 6), which may have been due to the higher mineral content of the litter and to differences in the physiology and age of the two fungi (Frankland, Lindley & Swift, 1978). The practical difficulties are illustrated by the variation in the values obtained when two different methods were used for measuring the biomass (Table 6). The levels of immobilisation were all biologically reasonable, but the higher values, obtained by hexosamine assay, were argued to be the more accurate.

Hyphal translocation (see Jennings: Chapter 5) can lead to the accumulation of nutrients in a decomposing organic substrate in amounts exceeding those in the living material. Net accumulation or loss depends on the balance between this translocation and a variety of other import or export activities and processes, including fungal sporulation,

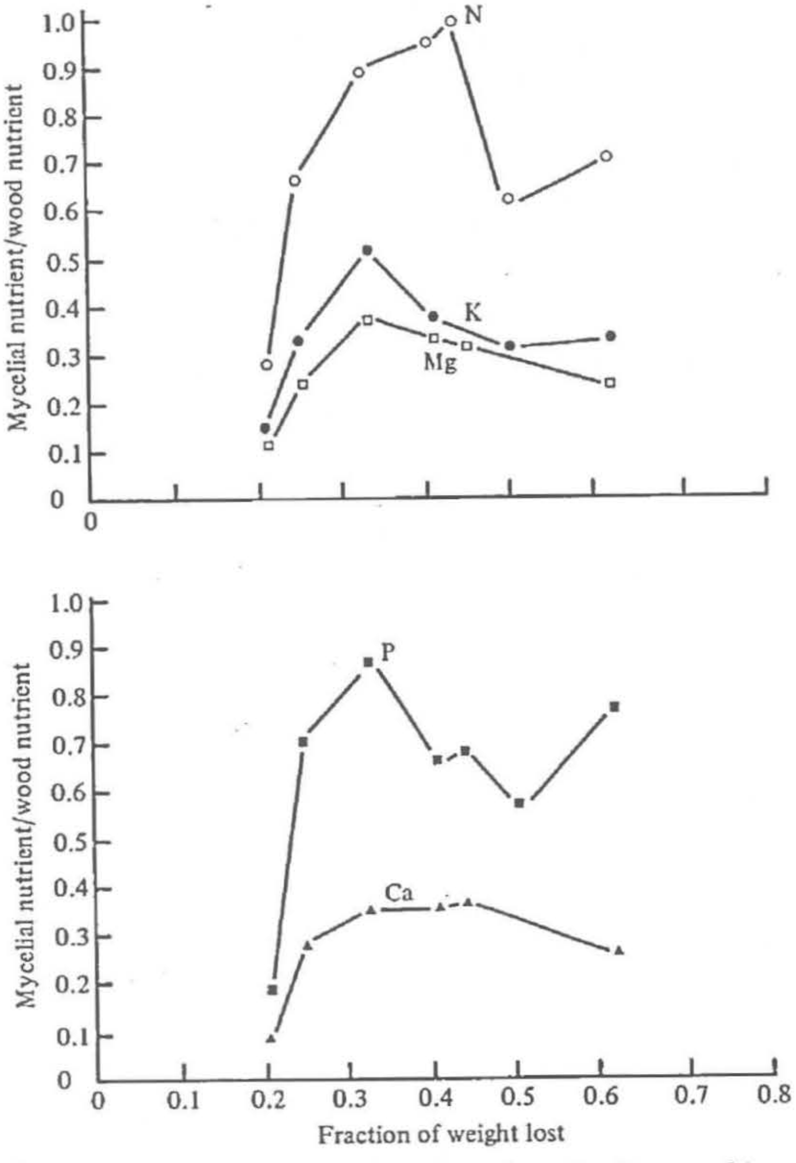

Fig. 2. Capture of mineral nutrients by *Stereum hirsutum* in *Quercus* branch-wood in relation to the state of wood decay. Capture expressed as the ratio of nutrient content (biomass × nutrient concentration) of the mycelium to the nutrient content of the wood. (From Swift, 1977*b*.)

Table 6. *Proportion of mineral nutrients immobilised in* Mycena galopus *after six months growth on sterilised leaf litter (percentage of the total amount in the substrate on an oven dry weight basis)*

		Method of biomass estimation ($n = 5$)	
Mineral nutrients	Litter	From hyphal length	By hexosamine assay
P	*Fraxinus*	16.7	43.4
	Betula	10.0	26.5
N	*Fraxinus*	6.9	17.9
	Betula	6.7	17.8
K	*Fraxinus*	6.3	16.4
	Betula	5.3	14.1
Mg	*Fraxinus*	4.1	10.3
	Betula	5.2	14.3
Ca	*Fraxinus*	2.4	6.4
	Betula	1.5	4.1

P, N, K: from Frankland, Lindley & Swift (1978).
Mg, Ca: J. C. Frankland & M. J. Swift (unpublished data).

animal migration and physical adsorption (Ausmus, 1977; Swift, 1977*b*). Swift found that the accumulation of nutrients in branch-wood decomposing on the floor of Meathop Wood depended on the type of decomposer. Significant net accumulation of nitrogen and calcium occurred in branches occupied principally by a mixed population of basidiomycetes, whereas branches at a similar stage of decay but occupied by wood-boring animals showed a net loss of nitrogen, phosphorus, calcium and magnesium (Table 7). A significant decrease in potassium in both cases was attributed to leaching of this very mobile ion. Nutrient accumulation was not evident when the branches were colonised by *S. hirsutum* alone (Fig. 2).

The jump from individual substrates to total ecosystem assessments of nutrient capture is made with a decrease in accuracy, but with this proviso in mind the exercise can give an overall picture of the relative status of particular groups of organisms. The pools of nitrogen, phosphorus and potassium in the living mycelium of the decomposer basidiomycetes of Meathop Wood, when estimated from the biomass values in Table 1, were approximately 9.5, 0.7 and 1.5 kg ha^{-1} respectively. These are small quantities in relation to the nutrient capital of a

Table 7. *Accumulation (+) or loss (−) of mineral nutrients* ($\mu g\ cm^{-3}$) *in branch-wood invaded principally by basidiomycetes or animals.* (After Swift, 1977*b*)

	N	P	K	Ca	Mg
Living wood ($n = 20$)	1057	69.5	767	1935	146
After invasion by basidiomycetes ($n = 26$)	+247*	−15.1	−626**	+1936**	−28
After invasion by animals ($n = 25$)	−347***	−41.7**	−746**	−158***	−88***

*, **, ***: significant at $P < 0.05$, < 0.01, < 0.001, respectively.

woodland but not necessarily so in terms of the nutrient cycles or throughflow. Harrison (1978) drew up a phosphorus budget for Meathop Wood and his figures for phosphorus contents of the soil, vegetation, fauna and micro-organisms are compared in Table 8 with estimates, derived from data in Table 1, of the reservoirs of phosphorus in the basidiomycetes and other fungi. The amount of phosphorus available in the soil, about 3 kg ha^{-1}, was low, but phosphorus *uptake* by the vegetation was at least 11 kg ha^{-1} yr^{-1}, so the plants must have depended heavily on the cycling of phosphorus in organic debris by the decomposers. The living vegetation contained about 45 kg P ha^{-1} compared with 4 kg P ha^{-1} in the living fauna and micro-organisms. About one-sixth or more of the latter was in the basidiomycetes.

Release of mineral elements by decomposer basidiomycetes

Release of nutrients by micro-organisms is as crucial as nutrient capital for the perpetuation of an ecosystem. The timing of this release is likely to be one of the most critical factors. A sudden flush of nutrients could result in heavy losses by leaching. In this respect basidiomycetes may well be important, at least in temperate woodlands, through the prolonged activity and resistance to decay (see Burges, 1960) of their mycelium. They are *habitués* rather than opportunists. Thus the group includes several psychrophilic or psychrotolerant species active both in summer and winter, even under snow (Hintikka, 1964), e.g. *Mycena galopus* which can reduce the dry weight of leaf litter *in vitro* by 8% ($P < 0.001$) in 6 months even at 4 °C (J. C. Frankland, unpublished). The generation time for many micro-organisms is only a few days,

Table 8. *Portion of a phosphorus budget for a temperate deciduous woodland, comparing higher-plant requirements for phosphorus and immobilisation of phosphorus in decomposer organisms (Meathop Wood, Cumbria, UK)*

P in the living biomass of trees, shrubs and ground flora[a]		45.0	kg ha^{-1}
P uptake by vegetation[a]		11.4	kg ha^{-1} yr^{-1}
P available in the soil[a]		3.0	kg ha^{-1}
P in the living biomass of the decomposers of plant debris and soil	fauna[a]	3.3	kg ha^{-1}
	basidiomycete mycelium[b]	0.7	
	non-basidiomycete mycelium[b]	0.3	
	bacteria and actinomycetes[a]	0.1	

[a] From Harrison (1978).

[b] Derived from biomass (Table 1) and percentage P in mycelium (basidiomycetes: 0.24; microfungi: 0.22).

whereas turnover and decay of *M. galopus* mycelium in Meathop Wood, for example, extended for 6 months or more (Frankland, 1975*a*). Nutrient release from the fruit bodies of basidiomycetes is likely to be more spasmodic, when they include extremely ephemeral and deliquescing forms. However, as Satchell (1974) pointed out when discussing soil invertebrates, it would be very difficult to demonstrate, in any particular situation, that retention of nutrients in biomass is more advantageous to an ecosystem in reducing leaching than it is disadvantageous in withholding plant nutrients.

Experimental evidence for nutrient release from organic matter by any type of micro-organism in the field is sparse. Like nutrient uptake it must be inferred, but fine feeder roots are often particularly well located in the organic horizons of a soil to receive any such release by decomposer basidiomycetes. Hintikka & Näykki (1967) reported a case where these roots were even more concentrated in humus containing basidiomycete mycelium than in the surrounding humus. Net release from the organic substrate will depend on certain critical levels in the concentrations of elements (Dowding, 1974; Heal, 1979). Thus, *M. galopus* utilised rather than released plant nutrients when it was grown on leaf litter for six months deprived of all external sources of mineral elements (J. C. Frankland, unpublished). Only water-soluble nitrate- and nitrite-nitrogen in *Quercus* litter increased under these conditions (Table 9). Indirect evidence of nutrient release by basidiomy-

Table 9. *Percentage gain (+) or loss (−) of water soluble mineral components of* Quercus *leaf litter after six-months incubation with* Mycena galopus *at 11 °C (n = 5)*

$(NO_3^- + NO_2^-) - N$	+ 33***
P	− 99***
$NH_4^+ - N$	− 76***
K	− 44***
Organic N	− 20***
Ca	NS
Mg	NS

*** Significantly different from controls, $P < 0.001$.
NS: not significantly different from controls.
Source: J. C. Frankland (unpublished data).

cetes in northern coniferous forests was obtained by Hintikka (1970), who found more available nitrogen and phosphorus in the so-called white-rot humus under various lignin-decomposing species of *Collybia, Marasmius* and *Mycena* than in the surrounding humus. Such remineralisation of nitrogen and phosphorus could be particularly important in forest soils, where these elements are usually less available than magnesium and potassium.

Nutrient release from the nutrient-rich sporulating tissues and substantial spore masses of basidiomycetes is again mainly conjecture from isolated observations. For example, Laursen & Miller (1977) suggested that a significantly large flush of nitrogen entered a tundra system from basidiomycete fruit bodies at snow melt. Similarly, Merrill & Cowling (1966) estimated that a single fruit body of *Fomes fomentarius* dispersed 34 g of nitrogen in its spores in 20 days, but the nutrient release from basidiospores to the soil depends on their wastage and decay rates, which are usually unknown.

Basidiomycetes may also mobilise nutrients from soil minerals by acid action. 'Weathering' of stones with disappearance of iron oxide has been observed, for example, under the mycelia of several basidiomycetes in a forest podsol by Hintikka & Näykki (1967).

Depending on its vitality, a basidiomycete can lose nutrients from its hyphae by various processes, including droplet excretion (Jennings: Chapter 5), leaching, lysis, autolysis and grazing. Healthy, living, mycelium is very resistant to leaching. When Stark (1972), for instance, exposed living rhizomorphs of basidiomycetes to leaching equivalent to a year's rainfall, 99.9% or more of the original content of nutrient elements was retained in the tissue. Whatever process of nutrient release occurs, recycling of the nutrients through animals and other micro-organisms in the habitat can follow, side-stepping uptake by plant roots. Even auto-recycling can occur. Levi, Merrill & Cowling (1968) found, for example, that some wood-destroying basidiomycetes could utilise nitrogen in their own mycelium, and they suggested that nitrogen was conserved in wood by its re-use from autolysed mycelium. Further indications of this were obtained from experiments in which white-rot fungi were found to be unique as a group in their ability to produce diffusible cellulases under conditions of nitrogen starvation (Levi & Cowling, 1969). Similarly, Merrill & Cowling (1966) suggested that several species of *Fomes* could retrieve nitrogen from the older hymenial layers of their perennial fruit bodies for re-use, since the nitrogen content of the layers decreased progressively with age. Nitrogen availability is now known to have far-reaching implications from the discovery that lignin degradation by basidiomycetes is regulated indirectly by nitrogen starvation (Kirk & Fenn: Chapter 4).

In tropical rain forests there is little available mineral in the soil, where it would be rapidly leached. This has led to the theory of direct mineral cycling (Went & Stark, 1968), which suggests that the abundant mycorrhizal fungi cycle minerals directly from dead organic matter to the living root with minimum release to the soil. In the Amazon forest area investigated by these authors, the mycorrhizas were chiefly of the non-basidiomycete endotrophic type, but Singer & da Silva Araujo (1979) found that some vegetation in Central Amazonia was rich in ectomycorrhizas. They discuss the occurrence of two basic types of tropical forest – ectotrophic and anectotrophic – one characterised by a prevalence of mycorrhizal basidiomycetes and accumulation of raw humus, and the other by saprophytic litter fungi including basidiomycetes, with the suggestion of two distinct patterns of mineral cycling. These observations draw attention to the disparity between the tropical and temperate scene, and to a need maybe for the two camps of mycologists, decomposer and mycorrhizal, to combine forces in research into nutrient cycling by basidiomycetes.

Supply of animal nutrients

The links between decomposer basidiomycetes and higher plants in nutrient cycling have been emphasised in this chapter, but basidiomycetes also provide a rich and digestible source of minerals for many animals besides the gourmet. Buller (1922) gave a particularly vivid account of Canadian squirrels hoarding stacks of fruit bodies in trees and attics, where the dry winter air delayed rotting. However, grazing of basidiomycetes by the microfauna rather than by vertebrates is probably of more relevance to the functioning of most woodland ecosystems. Grazing studies are now beginning at the microcosm level and show that complex competitive interactions and food preferences are involved (Parkinson, Visser & Whittaker, 1979; Newell, 1980). Basidiomycetes, however, may not contribute to animal nutrition via direct grazing alone. The recently formulated hypothesis on calcium cycling (Cromack *et al.*, 1977) implicates basidiomycetes, as accumulators of calcium and excretors of oxalic acid, in what could be a particularly important rôle. From field observations these authors concluded that the sparingly soluble calcium oxalate formed by fungi could be decomposed by the bacteria and actinomycetes of animal guts. The released calcium would then be utilisable by various invertebrates, such as microarthropods and earthworms, with high calcium requirements. The evidence was obtained from forest soils at pH 5–5.5; as J. P. Curry suggested in the discussion of their paper, this calcium contribution could be of even greater significance in very acid litter where calcium is severely limited.

In conclusion, therefore, the decomposer basidiomycetes are prominent in the organic horizons of many soils – the hub of biological activity. Here, they withdraw, store, accumulate and release mineral nutrients. By the very size of the hyphal production, these activities must have an impact on the ecosystem. Some of the most important facts relating to this rôle in mineral cycling have been outlined, but much research is needed to verify, quantify, and explain them.

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